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Ontogenetic Changes in Some Larval Characters of a Species Tentatively Identified to *Meristogenys amoropalamus* (Anura, Ranidae)

TOMOHIKO SHIMADA[1], MASAFUMI MATSUI[1]*, AND MARYATI MOHAMED[2]

[1] *Graduate School of Human and Environmental Studies, Kyoto University, Sakyo, Kyoto 606–8501, Japan*

[2] *Institute for Tropical Biology and Conservation, University Malaysia Sabah, Kota Kinabalu 88999, Sabah, Malaysia*

Abstract: Larval anuran jaw sheaths are corneous flat covers overlying the lateral surface of upper and lower jaws. Although most anuran tadpoles have a single sheath on both jaws, some have a pair of divided sheaths on one or both jaws, and sometimes both undivided and divided conditions are observed even within a species. We examined morphology of larval specimens tentatively identified as *Meristogenys amoropalamus*, collected from Borneo, and found that the lower jaw sheaths changed from a divided to an undivided state with larval development. Furthermore, the numbers of undivided rows of lower labial tooth, and of serrations of upper and lower jaw sheaths also changed ontogenetically. From these observations, we suggest that developmental stages should be taken into consideration when we use these larval characters for morphological comparisons in this genus.

Key words: Anuran tadpoles; Borneo; Jaw sheath; Labial tooth rows; Ontogeny

INTRODUCTION

Many anuran species are endowed with a corneous flat cover around the mouth, overlying the lateral surfaces of the upper and lower jaws (Fig. 1a, b), and equipped with black pigmentations and serrated edges. This structure, called "jaw sheath", is a transitory organ limited to the larval period, and disappears at the time of metamorphosis. Because anuran larvae lack true teeth, jaw sheaths are thought to serve as gouging, biting, and scraping structures (McDiarmid and Altig, 1999). Although each of the upper and lower jaw sheaths is usually found as a single plate, upper or both sheaths are separated into two parts in some species (McDiarmid and Altig, 1999). This separation has been used as a diagnostic character for some taxa (e.g., divided upper jaw sheaths for *Meristogenys* [Yang, 1991]: see below).

In some cases, however, both divided and undivided conditions are observed within a species. (e.g., *Ascaphus montanum*: Metter [1964] as *A. truei*; *Litoria wollastoni*: Menzies and Zweifel [1974]). Such examples suggest that the jaw sheaths might transform ontogenetically, but studies including sufficient num-

* Corresponding author. Tel: +81–75–753–6846; Fax: +81–75–753–2891;
E-mail address: fumi@zoo.zool.kyoto-u.ac.jp

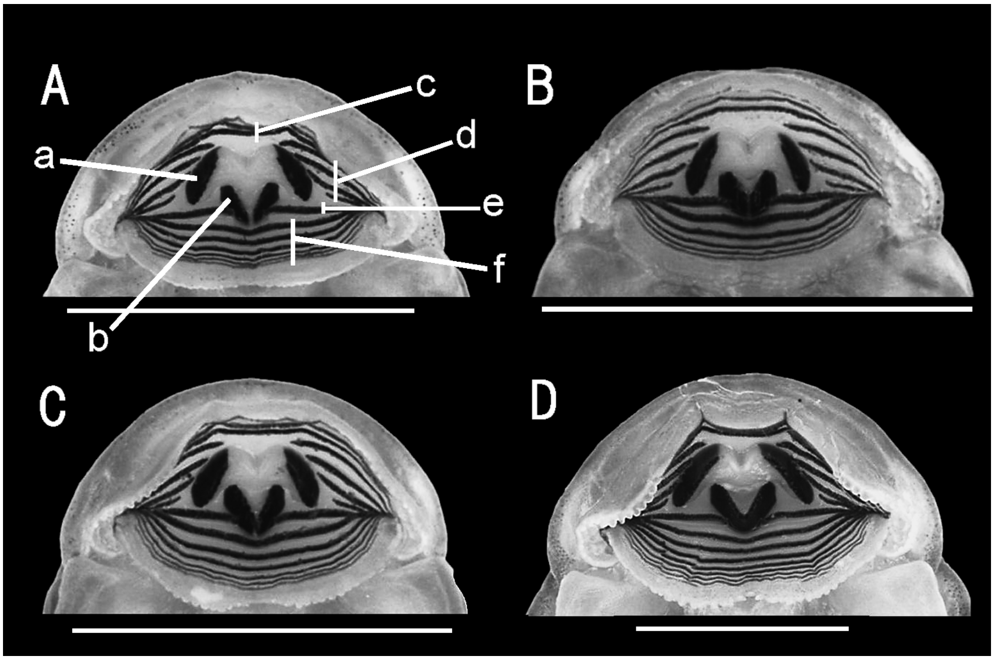

FIG. 1. Ventral views of the oral disks of *Meristogenys* larvae from Trus Madi, Sabah: (A) lower jaw sheaths divided (St. 27); (B) lower jaw sheaths connected with a sheet of thin corneous film (St. 26); (C) lower jaw sheaths connected by a narrow bridge (St. 26); (D) lower jaw sheaths completely fused (St. 37); (a) upper jaw sheath; (b) lower jaw sheath; (c) undivided rows of upper labial tooth; (d) divided rows of upper labial tooth; (e) divided row of lower labial tooth; (f) undivided rows of lower labial tooth. Scale bars=5 mm.

bers of specimens at various developmental stages are rare. In a ranid genus *Meristogenys* whose larvae have an abdominal sucker in adaptation to the swift current (Inger, 1966: Fig. 2h), Yang (1991) reported a species, which exhibited both conditions of larval jaw sheaths. In his collection, the youngermost two and the eldest one specimens of *M. amoropalamus* larvae had divided sheaths on the lower jaw, whereas specimens between them had an undivided lower sheath. This larval form was also collected by Shimada et al. (2007), but one difference was that division of the lower jaw sheaths in their specimens were actually incomplete, being connected by a sheet of thin film. Such a condition might represent an intermediate condition between divided and undivided sheaths. However, only four specimens were available for Shimada et al. (2007) then, and examination of more specimens of various developmental stages

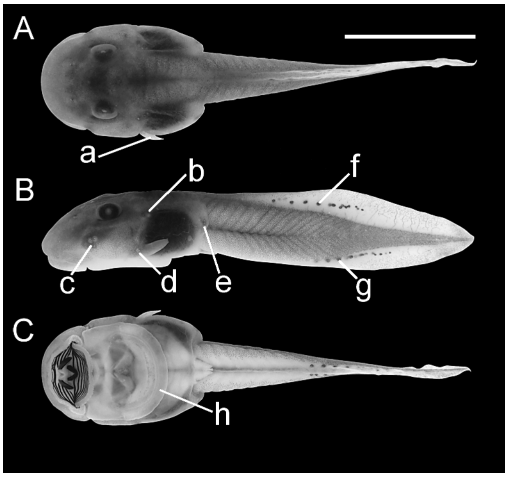

FIG. 2. Dorsal (A), lateral (B), and ventral views (C) of *Meristogenys* larvae from Trus Madi, Sabah (St. 30): (a) spiracle; (b) postorbital glands; (c) infraorbital glands; (d) prespiracular gland; (e) mid-lateral glands; (f) dorsal fin glands; (g) ventral fin glands; (h) abdominal sucker. Scale bar=10 mm.

remained crucial for any convincing conclusion.

In surveying amphibian collection in Universiti Malaysia Sabah, we found a series of larval *Meristogenys*. Through the morphological examination for this series, we identified them as larvae of "*M. amoropalamus*" according to Yang's (1991) description. However, we recognized distinct ontogenetic variation in some characters in this series, and closely studied them as reported below.

MATERIALS AND METHODS

A total of 72 uncatalogued specimens of Gosner's (1960) stages (Sts.) 26–41 collected by Robert F. Inger from Mt. Trus Madi, Tambunan District, Sabah, Malaysia (Borneo), during 9–15 September 1996 were examined. All these specimens are unidentified and stored in formalin of unknown concentration as BORNEENSIS collection of the Universiti Malaysia Sabah. We measured the head–body length (HBL) with a dial caliper to an accuracy of 0.1 mm, and recorded the conditions of the upper and lower jaws (Fig. 1a, b), the labial tooth row formula (Fig. 1c–f: McDiarmid and Altig, 1999), and the presence or absence of surface projections that are possessed by some *Meristogenys* larvae (Inger, 1966). The condition of the lower jaw sheath was classified into three categories: a single plate without any disjunction (Fig. 1D), a pair of completely divided plates (Fig. 1A), and the intermediate condition between these two (Fig. 1B, C).

In addition, we chose 28 specimens including a wide range of developmental stages and measured the following eight characters: (1) head–body width (HBW); (2) head–body height (HBH); (3) sucker width (SUW); (4) oral disc width (ODW); (5) snout width (SNW); (6) eyeball diameter (ED); (7) tail height (TLH); and (8) tail length (TLL: calculated by subtracting HBL from the total length; obtained only for specimens with a complete tail). We also counted the numbers of: glands on the postorbital (Fig. 2b), infraorbital (Fig. 2c), prespiracular (Fig. 2d), and midlateral (Fig. 2e) parts of the body, and on the dorsal (Fig. 2f) and ventral fin (Fig. 2g); and serrations on the upper (Fig. 1a) and lower jaw sheaths (Fig. 1b). We basically counted the body glands and the jaw sheath serrations on the left side. We used Spearman's rank correlations tests with the modification of the same ranks (Kendall and Gibbons, 1990) to test the correlations between developmental stages and the variations in morphological characters.

RESULTS

The ontogenetic change in HBL and the percentage ratios of each character to HBL are shown in Tables 1 and 2, respectively. All 72 specimens invariably had completely divided upper jaw sheaths. In contrast, the condition in the lower jaw sheath was variable in these specimens—completely divided in five (Fig. 1A), undivided in 49 (Fig. 1D), and in the intermediate conditions between them in 18 specimens. In 12 of these 18 specimens, right and left sheaths were connected by a sheet of thin light-brown corneous film (Fig. 1B), in other three, sheaths were connected by a narrow black bridge (Fig. 1C), and the remaining three had an almost completely fused single plate with a vertical medial crack on it. The relationships between conditions of the lower jaw sheath and developmental stages are shown in Fig. 3. Completely divided lower jaw sheaths were limited to the specimens of Sts. 26–28, while the specimens of St. 32 and greater stages had an undivided sheath. Intermediate conditions were found in larvae from Sts. 26 to 31. The condition of lower jaw sheaths (in the order of divided, intermediate, and undivided) significantly correlated with

TABLE 1. Growth in head–body length (in mm) of the *Meristogenys* larvae from Trus Madi, Sabah.

	Stage			
	26–29	30–33	34–37	38–41
$\bar{x}\pm2SE$	10.5±0.6	13.4±0.3	14.8±0.4	16.0±0.5
Range (N)	7.7–12.6 (22)	12.0–14.4 (21)	12.4–16.1 (19)	14.4–17.0 (10)

TABLE 2. Percentage ratio of each character to head–body length of *Meristogenys* tadpoles from Trus Madi, Sabah. See text for character abbreviations.

	Median	Range
HBW/HBL	63.7	58–68
HBH/HBL	33.8	31–38
SUW/HBL	57.6	55–62
ODW/HBL	46.7	44–55
SNW/HBL	54.2	51–59
ED/HBL	12.9	11–15
TLH/HBL	46.2	41–55
TLL/HBL	162.9	154–174

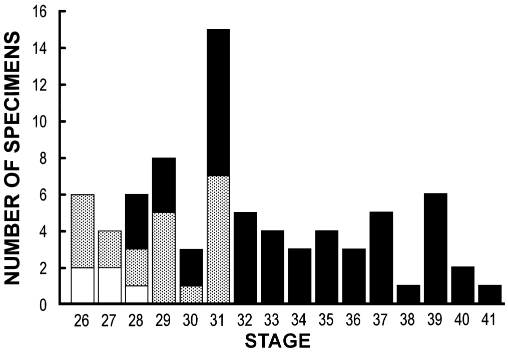

FIG. 3. Frequencies of the states of lower jaw sheaths in larvae at each developmental stage. Open box=two sheaths completely divided; grey box=two sheaths incompletely connected; closed box=two sheaths completely fused.

the developmental stages ($r=0.70$, $P<0.01$).

The numbers of serrations of jaw sheath were 6–17 in the upper half, and 6–13 in the lower half, both of which also correlated with the developmental stages ($r=0.87$, $P<0.01$ and $r=0.86$, $P<0.01$, respectively). The labial tooth row formula varied from 7(4–7)/5(1) to 7(4–7)/9(1, 9), and the number of undivided rows of lower labial tooth (Fig. 1f) also correlated with the developmental stages ($r=0.82$, $P<0.01$). The number of glands on the body was 2–4, 3–9, 0–3, and 1–9 in the postorbital, infraorbital, prespiracular, and midlateral area, respectively. There were no glands in the other parts of the head and body. The dorsal fin contained 7–28 glands, while the ventral fin had 6–22. None of the numbers of glands correlated with the developmental stages.

DISCUSSION

Because all specimens examined in the present study shared many characters, such as the absence of surface projections, presence of glands of both fins, and labial tooth rows of 7(4–7) on the upper jaw, we regard them as a single species. In this larval series, however, jaw sheaths were completely divided in younger individuals while they were completely undivided in older specimens with the intermediate conditions in-between (Figs. 1 and 3). This result strongly suggests that the condition of the lower jaw sheaths changes ontogenetically. Although the condition slightly varied within a given developmental stage, their connection began by St. 28 with a sheet of thin corneous film or a narrow black bridge between them, and finally the blank between them was narrowed into a medial vertical crack. After St. 32, all the specimens had a completely fused sheath on the lower jaw (Fig. 3). These characteristics were basically similar to those of "*M. amoropalamus*" in Yang (1991) and "*M.* sp." in Shimada et al. (2007). In Yang's (1991) collection, however, not only young specimens (Sts. 26 and 28), but also an old specimen (St. 41) had divided jaw sheaths. Although this division in older tadpoles was not observed in our sample, it can be regarded as a reduction of jaw sheath in relation to metamorphosis, because the jaw sheaths disappear when a tadpole transforms into a frog (McDiarmid and Altig, 1999).

Similarly, undivided rows of lower labial tooth and serrations of upper and lower jaw sheaths showed ontogenetic changes in numbers. These tendencies were also reported for *M. poecilus* (as *Amolops*) by Inger and Gritis (1983). On the other hand, labial tooth formula of the upper jaw, numbers of glands on the body and the fin, and presence or absence of surface projections did not correlate to the developmental stage in our specimens. Inger and Gritis (1983), however, reported that the number of glands in the ventral fin of *M. poecilus* increased as the individual developed, and Shimada et al. (2007) similarly found surface projections of some morphotypes of *Meristogenys* to increase in older larvae. These ontogenetic changes in larval characters can be obstacles to use them for taxonomic studies. However, because interspecific differences in morphological characters might be more pronounced in larvae than in adults in *Meristogenys* (Inger and Stuebing, 2005), we should make use of larval characters for the taxonomy of this genus, which is now in a serious mess. For this purpose, we must examine series of ample larval specimens across various developmental stages to confirm the degree of intraspecific ontogenetic changes in each character before interspecific comparisons.

The present result suggests that the lower jaw sheaths of *M. amoropalamus* (sensu Yang, 1991) derive from two (right and left) anlagen that are gradually fused into a single sheath. Although some larvae of *Meristogenys* (e.g. *M.* cf. *whiteheadi* and *M. kinabaluensis*) have a single sheath on lower jaw even at Sts. 26–28 (Shimada et al., 2007), these larvae might also show the same changes of jaw sheath in the course of their development before St. 26. If this is the case, the fusion of sheaths seen in this study may be interpreted as a variation in relation to heterochrony. To verify this inference, we should examine larvae before St. 26 of other *Meristogenys* species and confirm ontogenetic changes in this character at their early developmental stages.

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